

On Speciation in the Humid Tropics: some new data

by

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During the author's travels to Sri Lanka (Ceylon) and to Indonesia and, particularly, in the course of his examination of herbaria and botanical iconography pertaining to Dipterocarpaceae (see Foxworthy, 1927, 1932; Van Slooten, 1932, 1940, 1941, 1942, 1952; Symington, 1943; Ashton, 1962, 1964, 1967, 1969) he has already established many facts elucidating speciation in the humid tropics on the basis of the Law of Homologous Series in Hereditary Variation discovered as early as the beginning of this century by N. I. Vavilov (1920, 1922), elaborated by him somewhat later (1930, 1935) and subsequently by his numerous collaborators and pupils.

As is well known, Vavilov established this law mainly in the course of his studies on cultivated plants, his attention being attracted by their infraspecific diversity. But Vavilov had no opportunity to observe this phenomenon in a sufficiently large number of species of wild plants, nor those belonging to perfectly homologous genera.

Vavilov was sure that no homologous series of hereditary variation had been discovered in our wild holarctic genera and species merely because, in this respect, they had been extremely poorly studied.

In the Holarctic it is difficult to find homologous variation not only at the specific level, but at the infraspecific level as well. Many wild species occurring there appear to be surprisingly homogeneous. The cause of the apparent homogeneity is associated with their heterozygosity as has been pointed out by Vavilov himself (Vavilov, 1936, pp. 78-79) with cross-pollination, with the latent state of their recessive characters. However, the latent diversity of characters can be made apparent by means of compulsory self-pollination, or inbreeding. This fact is well known by all the geneticists and plant breeders.

Besides the actual homogeneity there is a delusive homogeneity. A conviction is very widespread among taxonomists about the perfect homogeneity of many widespread species over vast areas. The reason is that many botanists work mainly with herbarium material. The uniformity of herbarium specimens, sometimes accumulated in large numbers can be explained by the fact that many collectors involuntarily discarded specimens inconvenient on account of their dimensions or some other characteristics and thus made collections of standard specimens suitable for drying and mounting on standard sheets of herbarium paper.

As I know, tropical herbaria differ in this respect from holarctic ones. It is difficult to sort out series of standard samples in the tropics, even though the desire to do it be very keen, since many species, particularly large trees are so sparsely scattered in a tropical forest, that sometimes herbaria contain only their type or isotype specimens. This precludes the possibility of revealing infraspecific systems of hereditary forms in these plants by means of sheer observation even if they actually exist in nature.

There are at least a few genera of plants indigenous to the northern part of the Holarctic in which homologous series are observed not *within* species but

among the species of the given genus. Such are the genera *Verbascum* and *Celsia* (Scrophulariaceae) and *Astragalus* and *Oxytropis* (Leguminosae). It is true that here the taxonomic delimitation of these genera is not perfectly reliable, however.

The state of affairs in the humid tropics is very interesting. I venture to assert that, within the family Dipterocarpaceae, almost all the representatives of which are confined to tropical rain forests of Southern and South-Eastern Asia, the law of homologous series is conspicuous in all the genera and numerous species belonging to this family, including the monotypic genus *Upuna*, the single species of which, *U. borneensis*, also exhibits homology, at least in the leaf structure, as do the species of the other genera of this family.

It should be pointed out that Vavilov anticipated all this on the basis of his theoretical considerations with respect to plant taxa of almost any rank, having emphasized the universal significance of the law he had formulated, but practically he had no opportunity himself to encounter such interesting material for investigation as the Dipterocarpaceae.

The genetic affinity of the genera of Dipterocarpaceae is so close, that almost all the characters pertaining to the shape and structure of leaves, fruits and other organs and parts are subjected to homologous variation except the main generic characters felicitously designated by Vavilov as "generic radicals".

It is only the existence of such radicals, sometimes not quite distinct and also transgressive (e.g. genera *Shorea*, *Hopea*, *Doona*) that made it possible to classify the Dipterocarpaceae family, comprising a total of up to 580 species, into 15 genera.

Owing to the indistinctness of certain generic radicals (or, more precisely, unsuccessfully distinguished genera) taxonomists classifying Dipterocarpaceae were compelled to reduce to synonyms certain taxa described earlier at the rank of genus. Thus disappeared such generic names as *Pachynocarpus*, *Richetia* and some others.

When I am writing about the family Dipterocarpaceae, I have in mind only its Asiatic subfamily *Dipterocarpoideae* comprising the greatest number of genera and species, leaving aside for the time being the African subfamily *Monotoideae* (48 species of the genus *Monotes* and 4 species of the genus *Marquesia*), since I have not the necessary material at my disposal. The law of homologous series is manifest within the Dipterocarpaceae with the utmost distinctness and cogency in the first place in consequence of the numbers of species in many of its genera (see Ashton, 1964; Willis, 1966).

Shorea	...	...	180	Doona	...	...	11
Hopea (including Balanocarpus)	...	...	90	Parashorea	...	...	11
Dipterocarpus	...	...	76	Dryobalanops	...	...	9
Vatica	...	...	76	Cotylelobium	...	...	5
Vateria (incl. Stemonoporus)	...	...	21	Pentacme	...	...	3
Anisoptera	...	...	13	Monoporandra	...	...	2
	Upuna	...	...	1			

If all these genera of Dipterocarpaceae were arranged in a table following the sample of similar tables presented in Vavilov's works, it would at once become obvious that with respect to all the characters (studied up to the present time) species within each genus form homologous series.

The table does not show the combinations of characters of particular species, but only lists individual characters and their occurrence in the genera. Furthermore, they are only the most conspicuous ones, revealed either from herbarium material or from drawings published in the botanical literature. Many characters,

such as the leaf pubescence, the details of venation etc., are still to be studied. It is important to point out, that the characters of many species presented in the table were observed in isotype specimens a fairly great abundance of which is available in the Herbarium (LE) of the Komarov Botanical Institute of the Academy of Sciences of the USSR in Leningrad. The numbers of isotype specimens found there are 30, 15, 22, 13, 12, 5, 8, 3, 2, 3 and 2 for the genera *Shorea*, *Hopea*, *Dipterocarpus*, *Vatica*, *Vateria* (= *Stemonoporus*), *Anisoptera*, *Doona*, *Parashorea*, *Dryobalanops*, *Cotylelobium* and *Monoporandra* respectively. This is some guarantee against errors in the identification of numerous other specimens deposited in the Herbarium as 'ordinary' specimens and examined in the course of my investigations.

The table, the principle of composition of which is described here does not, of course, deal with the infraspecific homologous variation as yet unstudied at all in the representatives of the Dipterocarpaceae. My purpose was to demonstrate homologous series of species within genera, which in their turn are also homologous to the same extent. Thus, I do not merely repeat what has been done by Vavilov, but, as far as possible, endeavour to develop his theory.

Homologous characters are given in Latin terminology. The best illustrations of these characters might have been the drawings or photos, but, unfortunately they would have been too numerous and there would not be enough place for all of them in the table.

Unfortunately the names of the examined species not indicated are omitted but I hope I shall be able to add them in the very near future in a separate paper.

Similar to infraspecific systems of the forms of cultivated plants studied by N. I. Vavilov, the homologous characters in species belonging to the genera of Dipterocarpaceae exhibit in many cases independence of other characters, but in approximately 50% of species a rather distinct correlation is observed; for instance, between the characters of leaves on the one hand and, on the other the characters of fruits, with respect to their general similarity of appearance in the first place, and to their equal relative and absolute dimensions as well.

Being perfectly aware of the significance of the law he formulated, Vavilov quoted the remarkable, indeed prophetic, words of de Candolle (A. de Candolle, 1888, *La Phytographie*, p. 80) who wrote, that a day will come, when science will interpret the elements of a species as the elements of a genus, as the elements of a family, and all these groups will be coordinated according to a definite uniform system. Vavilov was perfectly justified in his conclusion: "This day has come" (Vavilov, 1936, p. 79).

The tropical family of arborescent plants, Dipterocarpaceae, is a good illustration for the ideas of Alphonse de Candolle and Nikolay Ivanovich Vavilov. All the taxonomic ranks of this family follow the law of homologous series that is common for all plants and, in fact, for all organisms. The genera of the Dipterocarpaceae are so closely allied to one another, that they can be regarded as initial species, as it were, evolved up to the generic level.

Thus, it is not only the infraspecific systems of hereditary forms of cereals, legumes, Cucurbitaceae and other cultivated plants, but also the species of gigantic tropical trees belonging to the Dipterocarpaceae that form homologous series. As it is illustrated by the example of this family, the Law of Homologous series in Hereditary Variation is directly associated not only with the initiation of new forms within a species as in the case of cultivated plants, where the action of the natural selection is superseded by artificial selection and where many forms and varieties of plants therefore have good chances for survival but also with speciation.

The obvious fact of the abundance of species characteristic of the genera of Dipterocarpoideae, particularly, of such genera as *Shorea*, *Hopea*, *Dipterocarpus*

and *Vatica* almost confined to the tropical rain forests of Southern and South-Eastern Asia should be explained.

Earlier I assumed (Fedorov, 1966) and this provoked some criticisms in the botanical literature (see Van Steenis, 1969, pp. 108-109; Ashton, 1969) that in a tropical rain forest the abundance and diversity of species within many genera and families of trees is explained by the fact that there natural selection does not eliminate indifferent characters; these characters remain in the populations, their frequency being governed by genetic drift. Of these forms possessing such characters, those having the rank of species survive. As it becomes clear at present, the possibility of initiation of such characters is afforded by the law of homologous series: being indifferent, they are homologous to the corresponding characters that are useful in certain closely allied forms. Despite the abovementioned criticisms of my views, I am still convinced, that if the speciation in the humid tropics was accomplished only by means of natural selection, without participation of genetic drift, there too, similarly to the northern zone of the Holarctic, each genus of wild plants would be represented by fragmentary group of species that would not form any perceptible homologous series.

One of the good examples of parallel (according to my concept, homologous) series, probably also formed by genotypic factors, within subgenera and other infrageneric taxa of the tropical genus *Ficus* having an extremely wide range (comprising about 900 species) is pointed out by E. J. H. Corner (1959, pp. 106-108), who designated this phenomenon, after Darwin, parallel evolution. Here the characters pertaining to the form of inflorescences and their position on a shoot are subjected to parallel (homologous) variation, as well as ramiflory and cauliflory and also geocarpy. The forms of growth or life forms in the subgenera of the genus *Ficus* also exhibit parallel (homologous) variation manifested in all the types from pachycaul trees to leptocaul trees. Epiphytic species of *Ficus* occur in at least three series. Creeping forms occur in five series in various combinations with epiphytic. Still more diverse are the homologous forms pertaining to the structure and venation of leaves, as well as to their size, both relative and absolute. Corner (*l.c.*) emphasizes that there can be no doubt in the convergent origin of all these forms, since parallel (homologous) species of different genera differ distinctly from one another in the structure of flowers, by the characters of which the main taxonomic subdivisions of the genus *Ficus* are delimited.

Corner makes an important reservation, that for instance, the case of a parallel (homologous) appearance of species of the genus *Ficus* with narrow leaves resembling the leaves of willow occur in the groups of the genus *Ficus* indigenous to different phytogeographical regions (Corner, 1961, p. 108; Corner, 1967, p. 33).

The same phenomenon in different families of tropical plants had already been mentioned by C. G. G. J. van Steenis (1948-1954, pp. LVII-LVIII).

As yet the mechanism of the origin of homologous series in different genera and families of plants in the humid tropics is not quite clear. The assumption that it is to a great extent based on mutagenesis leading to genotypic changes is quite justified, although, undoubtedly, many specific examples can also be phenotypic. Since allied species possess homologous characters, it is most probable that the genes responsible for these characters are also homologous or even identical at least within the same family. It was Vavilov himself (Vavilov *l.c.*) who referred to the facts of induction of artificial mutations in species of *Drosophila* that followed the law of homologous series.

Recombinations resulting from hybridization, serving, like mutations, as it were as raw material for natural selection, hardly played any significant role in speciation with respect to tropical trees, since hybrids occur rarely here (see Van

Steenis, 1969, p. 111). Chromosome numbers, for example, in different genera of the family Dipterocarpaceae, the object of my interest, in many cases prove to be the same. In most species of the genus *Dipterocarpus* studied (as yet not many) the prevailing chromosome number is $2n = 20$ (see Fedorov, ed. 1969, p. 262; Moore, ed. 1973, p. 274).

Corner (1954, pp. 33-34) was the first to assume that selfpollination prevails in the trees of tropical rain forests. Later I advanced a similar hypothesis (Fedorov, 1966) although I overlooked Corner's priority. Quite recently, as the result of the investigations of Bawa (1974), as well as of Bawa and Opler (1975) various types of pollination became known for both the tropical and temperate regions. By the way, it was revealed, that many trees apparently having bisexual flowers are actually dioecious in many cases, since either gynoeceum or androeceum prove to be underdeveloped, or their development proves to be asynchronous. Other details of the "reproductive biology" as it is designated by these authors and Ashton have been elucidated. Ashton quite recently published (Ashton, 1975, p. 109) an abstract of a paper on the existence, in tropical rain forest trees, of both panmixis and apomixis. It should be pointed out, that all the details of these phenomena in Tropics are as yet insufficiently studied by far, but only one fact, but a most the important one, should be apparently recognized to be beyond doubt: interspecific hybridization is a very rare event in tropical rain forests.

Nature itself has established many almost insuperable obstacles to spontaneous hybridization between species of tropical trees which would lead to heterozygosity. This fact was mentioned in my earlier paper (Fedorov, 1966). The difficulty of such hybridization is, in the first place, the consequence of non-coincidence of the time of flowering, particularly, in the equatorial zone where there are no seasons of the year. This non-coincidence is observed even among individuals belonging to the same species, let alone those belonging to different species; another obstacle is the prolonged and irregular period of sterility, sometimes lasting for several years, then the low population density of many species, up to almost perfect dissociation of separate individuals of these species, i.e. their spatial isolation, and also biotic isolation and, in general, the diversity of biological niches.

The survival of a large number of species belonging to the genera of Dipterocarpaceae and their resistance to the pressure of natural selection can be explained by the early development of isolation from one another of the most diverse types. This problem was successfully studied by P. W. Richards (1969, pp. 149-153) and by F. R. Fosberg, who delivered a paper on this topic at one of the symposia of the XIth International Botanical Congress held in Seattle (Fosberg, 1969, p. 62).

Th. G. Dobzhansky (1950, pp. 219-221), in his study especially devoted to the problem of evolution in the tropics, correctly emphasizes, that in the temperate and in the cold zones such elementary factors as the sufficient or insufficient quantity of food and the degree of resistance to low winter temperatures played the most important rôle in the process of natural selection. In the humid tropics the interrelations with the environment are more complicated; its requirements are more refined, while the response of organisms is more diverse and complicated; the rôle of the biotic environment is significantly more important, than in temperate and cold regions.

Polyploidy, apparently, also played a certain role in the speciation in tropical trees. At least polyploids have been found in some species belonging to the families Leguminosae, Simaroubaceae, Meliaceae, Anacardiaceae, Sapindaceae, Bombacaceae, Sterculiaceae and to some other families, represented in the flora of tropical semideciduous forests of Costa Rica (Bawa, 1973, pp. 422-434). However, polyploid series are very rare in these cases.

The counts of chromosome numbers in species belonging to the genera of Dipterocarpaceae were commenced only quite recently. Chromosome numbers have been determined for only thirty species (see Fedorov, ed. 1969, p. 262; Moore, ed. 1973, p. 274). If it is remembered that this family comprises 580 species, it would be clear, that any conclusions concerning the rôle of polyploidy in the evolution of this family would be as yet premature. Nevertheless, the prevailing chromosome number being $2n = 20$ (genus *Dipterocarpus*), cases have already been recorded of diverse numbers in certain species of the genus *Shorea*, where the chromosome number is $2n = 14$ or 28. There are cases when $2n = 12$ (*Pentacme*), while in the genus *Dipterocarpus* rarely occur species with $2n = 30$. The main "x" numbers in different genera of the family are probably close to 5-7-11.

It is possible to interpret from a new point of view the phenomenon of convergence, which is very conspicuous and widespread in the trees of a tropical rain forest. This convergence pertains to the shape of leaves, inflorescences and other parts of plants belonging to different genera and families, particularly in the tropical Lauraceae, Annonaceae, Sapotaceae, Fagaceae and many others. This convergence is adaptive, but probably it is based on the law of homologous series in hereditary variation as dealt with in this paper.

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		Shorea	Hopea	Dipterocarpus	Vatica	Vateria	Anisoptera	Doona	Parashorea	Dryobalanops	Cotylelobium	Pentacme	Monoporandra
1	Folia late-elliptica vix acuminata, obtusa vel retusa ca 20 cm. longa et 15 cm. lata	+	+	+	+	+			+				
2	Praeced. similia, ca 10-15 cm. longa et 5-7 cm. lata	+	+	+	+	+	+	+	+		+	+	
3	Praeced. similia, ca 5-10 cm. longa et 3-5 cm. lata	+	+	+	+	+	+	+					
4	Folia oblongo-elliptica vix acuminata, ca 25-35 cm. longa et 10-15 cm. lata	+	+	+	+	+		+					
5	Praeced. similia, ca 10-15 cm. longa et 3-7 cm. lata	+	+	+	+		+	+		+	+		

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		Shorea	Hopea	Dipterocarpus	Vatica	Vateria	Anisoptera	Doona	Parashorea	Dryobalanops	Cotylelobium	Pentacme	Monoporandra
6	Folia late-ovata acuminata, ca 10-15 cm. longa et 6-8 cm. lata	+	+	+									
7	Praeced. similia, ca 5-10 cm. longa et 3-7 cm. lata	+	+	+	+			+	+				
8	Folia obovata vix acuminata, 10-20 cm. longa et 5-6 cm. lata	+		+	+	+	+						
9	Praeced. similia, ca 3 cm. longa et 2 cm. lata	+		+	+								
10	Folia obovata obtusa, ca 4.5 cm. longa et 3 cm. lata	+		+	+	+							
11	Folia rotunda obtusa, ca 15 cm. longa et lata			+									
12	Folia rotunda vix acuminata, ca 15 cm. longa et lata	+		+									
13	Folia fere rotunda vix acuminata, ca 3 cm. longa et 2.8 cm. lata		+										
14	Folia late lanceolata acuminata, ca 20 cm. longa et 5 cm. lata	+	+		+	+							
15	Praeced. similia, ca 7 cm. longa et 4 cm. lata	+	+		+			+		+			
16	Folia elliptica apice caudata, ca 7 cm. longa et 3 cm. lata	+	+		+	+		+		+			+

Homologous characters		Genera Dipterocarpacearum											
		1	2	3	4	5	6	7	8	9	10	11	12
		Shorea	Hopea	Dipterocarpus	Vatica	Vateria	Anisoptera	Doona	Parashorea	Dryobalanops	Cotylelobium	Pentacme	Monoporandra
17	Praeced. similia, ca 6 cm. longa et 2-3 cm. lata		+		+	+		+					
18	Folia late ovata apice caudata, ca 6 cm. longa et 2.5-3 cm. lata		+		+	+		+		+			
19	Folia oblanceolata obtusa, ca 10-15 cm. longa et 4.5 cm. lata				+		+						
20	Praeced. similia, ca 3-5 cm. longa et 1-3 cm. lata	+											
21	Folia basi subcordata	+				+						+	
22	Folia basi truncata	+	+	+	+	+	+	+		+			
23	Folia basi rotundata	+		+								+	
24	Folia basi cuneata	+	+	+									
25	Lamina foliorum omnino glabra	+	+	+	+	+	+	+	+	+	+		
26	Lamina foliorum plusminusve pilosa, tomentosa vel hirsuta	+		+	+			+					
27	Fructus magni, ca 10-15 cm. longi	+		+			+		+	+			
28	Fructus mediocres, ca 5-7 cm. longi	+	+	+	+		+	+	+	+	+		
29	Fructus parvi, ca 2-3 cm. longi	+	+	+	+			+	+	+	+		
30	Calycis lobi post anthesin accrescentes	+	+	+	+	+	+	+	+	+	+	+	+
31	Calycis lobi abbreviati, fructus globosi	+	+	+	+	+			+	+			

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